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MECHANISTIC POPULATION MODELS IN BIOLOGY: MODEL DERIVATION AND APPLICATION IN EVOLUTIONARY STUDIES

by

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Abstract

In general, models of ecological systems can be broadly categorized as 'top-down' or 'bottom-up' models, based on the hierarchical level that the model processes are formulated on. The structure of a top-down, also known as phenomenological, population model can be interpreted in terms of population characteristics, but it typically lacks an interpretation on a more basic level. In contrast, bottom-up, also known as mechanistic, population models are derived from assumptions and processes on a more basic level, which allows interpretation of the model parameters in terms of individual behavior.

Both approaches, phenomenological and mechanistic modelling, can have their advantages and disadvantages in different situations. However, mechanistically derived models might be better at capturing the properties of the system at hand, and thus give more accurate predictions. In particular, when models are used for evolutionary studies, mechanistic models are more appropriate, since natural selection takes place on the individual level, and in mechanistic models the direct connection between model parameters and individual properties has already been established.

The purpose of this thesis is twofold. Firstly, a systematical way to derive mechanistic discrete-time population models is presented. The derivation is based on combining explicitly modelled, continuous processes on the individual level within a reproductive period with a discrete-time maturation process between reproductive periods. Secondly, as an example of how evolutionary studies can be carried out in mechanistic models, the evolution of the timing of reproduction is investigated. Thus, these two lines of research, derivation of mechanistic population models and evolutionary studies, are complementary to each other.

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List of original publications

This thesis is based on the following articles and manuscripts, referred to in the text by their Roman numerals:

I Eskola, H.T.M. and S.A.H. Geritz (2007). On the mechanistic derivation of various discrete-time population models. *Bulletin of Mathematical Biology* 69, 329–346.

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V Eskola, H.T.M., S.A.H. Geritz and M. Gyllenberg. On the evolution of the timing of reproduction with non-equilibrium resident dynamics. *Submitted manuscript*.

Contents

Part I

General theory

1 Introduction

In 1202 AD, Leonardo Pisano, nowadays commonly known as Fibonacci, posed the following question in his arithmetic book *Liber Abaci* (quote from Sigler (2002)):

> *"A certain man had one pair of rabbits together in a certain enclosed place, and one wishes to know how many are created from the pair in one year when it is the nature of them in a single month to bear another pair, and in the second month those born to bear also."*

This must be one of the first individual-based population models in the history of mathematics. It describes the behavior of the individuals, and the population dynamics is then derived from the individual-level processes. If we denote the number of rabbit pairs at the reproductive period t by N_t, we then have

$$N_{t+1} = N_t + N_{t-1}, \quad t = 1, 2, 3, \ldots,$$

which of course gives with $N_0 = N_1 = 1$ the famous Fibonacci sequence

$$1, 1, 2, 3, 5, 8, 13, \ldots.$$

Fibonacci himself did not give the solution to this problem in a closed form, but explains how to iterate the process to achieve 377, the number of rabbit pairs after one year. Of course, the real beauty of the model lies in the ratio of successive Fibonacci numbers, $N_t/N_{t+1} \approx (\sqrt{5}-1)/2$ for large t, the so-called golden mean. In addition to representing ideal beauty in classical paintings, it can also be found in, for example, sunflower heads and pine cones, and many other plants. This hints to the possibility of surprisingly simple processes creating complexity (and beauty) on larger scale.

In general, a widely used continuous-time model for a single species is a differential equation of the form

$$\frac{dN}{dt} = f(N),$$

where $N(t)$ is the population density at time t and the function f gives the rate of change per time unit. Alternatively, in discrete time population models are often difference equations of the form

$$N_{t+1} = g(N_t),$$

where N_t is the population density at time t. The task of a modeler is then to find the corresponding function f (or g) describing the population dynamics. If, as in the Fibonacci example explained above, the function is based on individual behavior, it can be called a *mechanistic* model. If, on the other hand, the function is chosen more on the basis of simply describing the dynamics on the population level and without an interpretation on the individual level, it can be called a *phenomenological* model. (The difference is treated in more detail in Section 2.)

In the history of mathematical biology, the majority of models have been of the phenomenological type (see, for example, Kingsland (1995) for an overview of the development of population ecology). A famous example is the so-called *logistic growth model*,

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right),$$

where r is the population's intrinsic rate of increase and K the carrying capacity, i.e. both r and K are population parameters. The model is also sometimes called the *Verhulst-Pearl* model. It was originally proposed by Verhulst (1845), and later on advertised by Pearl (1925) as a universal law of population growth, even though no justification based on underlying mechanisms was given. After that, the model has been widely used to describe self-regulated populations, and today there are also several mechanistic explanations in different ecological contexts available (see, for example, Rueffler et al. (2006) for a list of references). However, nowadays no one would call the logistic growth model, or any other mathematical model, a 'universal law', because it is widely appreciated that no model can ever be more than a simplification of the reality. Nevertheless, because of their link to lower-level processes, individual-based models might still have a greater ability to help understand the properties of the target system.

In recent years, there has been increasing interest in individual-based models. One reason might be simply that the dramatically increasing computing power has also enabled the numerical treatment of more complex models. Also, it has been realized that in order to have meaningful results from evolutionary studies, the underlying processes should be explained in individual terms (see Section 2.3). However, we are still far from the 'mechanistic-ecological utopia' envisioned by Schoener (1986) in his review article.

2 Mechanistic models

2.1 Definitions

The label 'mechanistic' in the context of population ecology means that a model is formulated in terms of individual processes (see, for example, Schoener (1986)). The logic behind the terminology is of course that the model describing the dynamics on the population level is based on mechanisms at a lower hierarchical level. In population ecology this is usually the individual level, but the same terminology is also used in, for example, the biomedical sciences, where the focus may be on the cellular or molecular level. As an alternative, the names 'first principles derivation' or 'bottom-up derivation' are also used for the concept.

The structure of a phenomenological (or 'top-down') population model can be interpreted in terms of population characteristics, but it typically lacks an interpretation on a more basic level. For example, a phenomenological model may contain parameters such as the 'intrinsic rate of increase' or the 'carrying capacity', but their relationship to the characteristics of individuals that make up the population is unclear. In contrast, parameters in a mechanistic population model can be interpreted in terms of the behavior of the individuals.

2.2 The modeler's fundamental problem: biological realism *vs.* mathematical tractability

Mathematical models are always simplifications of the real world. Any attempt to capture all of the complexity of the target phenomenon is doomed to fail, and the modelling procedure is necessarily a compromise between mathematical tractability and biological meaningfulness. Phenomenological models are often at one end of the spectrum, aiming at a description with only a few 'mega-parameters'. The other end of the spectrum includes, for example, complicated individual-based models of ecological communities, in which physiological phenomena and interspecies interactions are included in high detail, but which can only be treated numerically. One such an example is a study by Hassell et al. (1999), considering budworm outbreaks affecting the competition between fir and birch trees. (The original model includes over 80 variables and parameters, but the system is after several simplifying assumptions finally squeezed into three equations apparently capturing the essential dynamics.) In phenotypic population models, the focus is often on behavioral processes, and physiological, biochemical, etc. detail is omitted in order to get at least some analytical results. Both approaches, phenomenological and mechanistic modelling, can have their advantages and disadvantages in different situations. For example, the specific form of a phenomenological model is often chosen based on a mathematically convenient form, or flexibility in statistical data fitting. However, mechanistically derived models might be better at capturing the properties of the system at hand, and thus give more accurate predictions (see, for example, Schoener (1986), DeAngelis and Gross (1992)). In particular, when

the models are used for evolutionary studies, it is more appropriate to use mechanistic models, since selection takes place on the individual level, and in mechanistic models the direct connection between model parameters and individual properties has already been established.

2.3 Mechanistic models and evolutionary studies

Selection acts on individuals. There are heritable differences between individuals of a species, which result also in differences in the survival and reproductive success of individuals. Because of natural selection, the genetic composition of a population will change in the course of time. There have also been contrasting views of the level that selection is working on, the strongest alternatives being genes and groups. (For example, Dawkins (1976, 1981) promotes the gene level, or 'the selfish gene' view, and Lewontin (1983) criticizes it. Considering the 'group selection' view, see, for example, Wynne-Edwards (1962) promoting it and Williams (1966) for criticism.) However, the current consensus has settled on the individual as the primary unit of selection.

'Selection on the individual' refers to selection on the phenotype. Even though evolution ultimately takes place on the DNA level, the mapping between genotype and phenotype is seldom simple, and often also depends on the environment an individual is experiencing. Therefore, in mechanistic population models genetic accuracy is usually sacrificed, and the evolutionary success of phenotypes is studied instead (see Section 4). However, since the model parameters in mechanistic models are already linked to individual behavior, evolutionary studies are also better based on models with a mechanistic derivation. In some cases, it can even be misleading to study directly the evolution of mega-parameters without a connection to processes on the individual level (see, for example, Bowers et al. (2003), Rueffler et al. (2006)).

2.4 Models with the Allee effect

The name 'Allee effect' comes from the work W. C. Allee did on the cooperative behavior of animals (Allee (1931, 1938), Allee et al. (1949)). Allee effects occur when individuals benefit from the presence of conspecifics, and as a result suffer a decline in some component of fitness when populations become small or sparse (Stephens et al., 1999). Strong Allee effects can lead to threshold population densities below which the population growth is negative, making extinction likely. Many mechanisms can lead to Allee effects. To use the distinction emphasized by Berec et al. (2007) and Courchamp et al. (2008), *component Allee effects* mean a reduction in a component of fitness with decreasing population density caused by a single mechanism, whereas *demographic Allee effects* mean the total reduction in fitness, resulting from all the different component Allee effects and negatively density dependent mechanisms affecting the population. Component Allee effects can be caused by, for example, mate finding or predator dilution (Courchamp et al.,

2008), and all the component Allee effects together might then translate into a demographic Allee effect on the population level, usually measured by the per capita population growth rate.

In recent years, the concept of the Allee effect has experienced a kind of renaissance, resulting in several papers and a book (Courchamp et al., 2008). (Reviews can be found in, for example, Boukal and Berec (2002) and Gascoigne and Lipcius (2004).) This is no surprise, since the phenomenon has great importance in, for example, conservation ecology, sustainable harvesting, control of invasive species and pest control (see, for example, Berec et al. (2007), Courchamp et al. (1999), Stephens and Sutherland (1999), May (1977)). However, most of the models treated in the literature are phenomenological models, in which the Allee effect is merely incorporated by means of a term with convenient mathematical properties, leading to negative growth rates at low population densities. The same motivation for using mechanistic models as already explained above also applies in systems with Allee effects, maybe even more so, since the threshold densities might be strongly dependent on individual-level processes. Phenomenological models usually obscure this connection, which can lead to erroneous management decisions, proving fatal for, for example, an endangered species.

3 Model derivation

In this section, the methods to derive mechanistic population models used in this thesis are explained.

3.1 Semi-discrete models

In general, mathematical population models can be divided into two categories depending on whether time is considered to be continuous or discrete. If generations are overlapping and births and deaths happen throughout the year, a continuous model might describe the system more accurately, and the model is built on differential equations. In contrast, if the studied population is semelparous and reproduces only in discrete instants, a discrete model might be more appropriate, resulting in difference equations. However, in nature organisms rarely exhibit such clear-cut phenomena, and most populations experience both continuous and discrete processes.

One way to solve this problem is to use models that are combinations of both continuous and discrete processes. That is, the model has continuous *within-season* (or *within-year*) *dynamics*, which includes, for example, competition, mortality, and reproduction. The within-season dynamics between different seasons are then tied together with the *between-season* (or *between-year*) *dynamics* in the way that the 'output' of the between-season dynamics of one season is the 'input' of the within-season dynamics of the next year. For such models, the name 'semi-discrete' has been proposed by Pachepsky et al. (2008) and Singh and Nisbet (2007).

One way to implement the within-season dynamics is to use so-called *site-based models*, which have been used to investigate the effects of the types of competition and individual distribution on population dynamics. In site-based models, individuals are assumed to be distributed randomly to sites where they reproduce and interact locally. Surviving offspring then become the next generation and are again distributed to the sites at random. The interaction processes between the individuals on the sites, together with the distribution of the individuals, then define the resulting discrete-time model. Examples of site-based models can be found in, for example, Sumpter and Broomhead (2001), Johansson and Sumpter (2003), Brännström and Sumpter (2005) and Anazawa (2009). Another possibility is to explicitly model the continuous within-season dynamics with differential equations, which method has been used in this thesis. The main difference between these two approaches is thus in the way that temporal and spatial processes within the reproductive season are taken into account. In site-based models, the temporal processes are ignored, whereas the spatial distribution of individuals is included in the model. In contrast, in the modelling approach used in this thesis, the spatial structure is not included in the models, but the temporal processes during the season are modelled explicitly.

3.2 Models with explicit, continuous within-season dynamics

In this thesis, the continuous, individual-level interaction processes of the within-season dynamics are modelled using the *law of mass action*. The mass action principle has its origins in chemical reactions, and it simply says that the rate of a reaction is proportional to the product of the concentrations of the reactants. Consider, for example, a *bimolecular reaction*,

$$A + B \xrightarrow{k} \text{products},$$

where a collision between molecules A and B is required for the formation of some product molecules. Then, the mass action principle says that, if A and B also denote concentrations, the changes in the concentrations can be modelled by

$$\frac{dA}{dt} = \frac{dB}{dt} = -kAB.$$

As such, the law of mass action is a result simply describing the behavior of a population of molecules. However, its use can also be mechanistically justified, if individual molecules are considered by means of a continuous-time stochastic model; see, for example, Bharucha-Reid (1960) for a detailed derivation in this context.

In population ecology, the interactions between individuals can be perceived as analogous to molecular reactions, and the mass action principle thus applied also in this context (see, for example, Murray (2002), Thieme (2003)). As an example, predation between prey N (with density n) and predator P (with density p) happening with the rate a could be modelled with the reaction

$$N + P \xrightarrow{a} P,$$

and the change in the prey density then corresponds to the differential equation

$$\frac{dn}{dt} = -anp.$$

In nature, a population is usually under the influence of several different processes. For example, there might also be another prey type M (with density m), which both the predator P and the other prey type N are feeding on with the rates b and c, respectively. These assumptions translate into a *reaction network*

$$\begin{aligned} N + P &\xrightarrow{a} P, \\ M + P &\xrightarrow{b} P, \\ M + N &\xrightarrow{c} N, \end{aligned}$$

which can be modelled with a system of differential equations

$$\begin{cases} \frac{dn}{dt} = -anp, \\ \frac{dm}{dt} = -bmp - cmn. \end{cases}$$

However, the number of equations easily grows very large when a complicated system with many reactions is modelled. Therefore, ways to reduce the number of equations are also needed. One possibility is to see if the population exhibits a *conservation law*, i.e. if the total population size remains constant even though individuals may be in different states. Another example of a standard tool is *time-scale separation*. The method is based on the observation that some reactions may be fast or slow compared to others. The relative changes in the corresponding quantities then take place on different time-scales, and a fast system can be assumed to always be on a *quasi-equilibrium*.

More on the basic modelling methods can be found in, for example, Murray (2002) and Thieme (2003). Of course, it must be realized that also models based on the mass action principle make simplifying assumptions, such as infinite numbers of reacting particles in a well-mixed medium. Nevertheless, they give an approximation for the effects of inter-individual processes, and are thus one option for the derivation of mechanistic population models.

4 Evolutionary studies

Ever since Darwin (1859) introduced the concept of *natural selection*, scientists have tried to understand the evolutionary processes shaping the biological world. Later on, the actual inheritance mechanism carrying information through generations, the DNA, was found and introduced by Watson and Crick (1953), but unfortunately this discovery did not yield simple answers, either. Selection acts on phenotypes, and usually the mapping from the genotype to the phenotype is either fully unknown or at least very complicated. Moreover, sexual reproduction also involves mating, which adds further difficulties into understanding evolutionary processes.

Hence, simplifying assumptions are needed, and the investigation has proceeded in two main directions. The framework of *quantitative genetics* focuses on the genes. The other alternative is to ignore the genes (and sex) altogether and study phenotypic evolution with clonal reproduction, and variability is simply assumed to be generated through mutations. This is what the *adaptive dynamics* framework does. (For example, Abrams (2001) compares these methods.)

4.1 The adaptive dynamics framework

The adaptive dynamics framework is an approach to studying the evolution of phenotypic traits in a population, for which the population dynamics is given by a dynamical system. The approach has its roots in *evolutionary game theory* (see, for example, the classical book by Maynard Smith (1982)), and it aims at studying evolutionary change when selection is density and/or frequency dependent. The framework was originally presented by Metz et al. (1992, 1996) and Geritz et al. (1997, 1998) (see also the general introduction by Diekmann (2004)), and its main properties are introduced below.

4.1.1 General assumptions

The adaptive dynamics framework makes the following general assumptions (Metz et al. (1996), Geritz et al. (1998), Geritz and Gyllenberg (2005)).

(i) Individuals reproduce clonally.

(ii) The ecological and evolutionary time-scales are separated.

(iii) The initial mutant frequency is small in a large resident population.

(iv) Mutational steps are small.

As a starting point, the framework assumes a *monomorphic* population, i.e. a population consisting of individuals that all have the same phenotype x in the *strategy space* X. The traditional adaptive dynamics framework assumes scalar strategies, i.e. $X \subset \mathbb{R}$, but the more recent theoretical generalizations also treat

multi-dimensional strategies (see, for example, Geritz (2005) and Section 4.2). The *population state space* is denoted by M, and population growth is described by a dynamical system. If a continuous-time population model is used, the dynamical system is often given by a differential equation, $\frac{d}{dt}N = f(N, x)N$, where $N(t)$ is the population density at time t. Correspondingly, if a discrete-time model is used, the dynamical system is often given by a difference equation, $N_{t+1} = f(N_t, x)N_t$, where N_t is the population density at time t.

Key issues in adaptive dynamics studies are the concepts of *fitness* and *invasibility*, which will be addressed in more detail in the following section. In addition, a standard tool of graphical analysis, the *pairwise invasibility plot*, is introduced.

4.1.2 Invasion fitness of a mutant

The concept of fitness was for a long time a source of debate in the biomathematical literature (see, for example, the review by Brommer (2000)). On the one hand, the question as to what quantity should be used to measure an individual's fitness divided opinions. On the other hand, natural selection was conceived as a pure optimization process, which has yielded several models of simply optimizing some aspect related to an individual's survival, such as the energy uptake (see, for example, Alexander (1996)). In the 1990s, however, the focus shifted to the invasibility properties (Metz et al. (1992), Rand et al. (1994)), which has resulted in a consensus on the fitness concept. Also, the question of optimization has been clarified (Metz et al., 2008b,a) further.

Metz et al. (1992) defined in ordinary population models the *fitness* of an individual as the long-term exponential growth rate of a phenotype in a given environment. In particular, the adaptive dynamics framework uses the concept of *invasion fitness*. It describes the behavior of a population of an initially rare mutant, termed the *invader*, in the early stages of *invasion*, when the population density of the mutant type is still low and any effect of the invader on the environment set by the predominant population, termed the *resident* population, can be neglected. Let $r(x, E)$ be the long-term exponential growth rate of the phenotype x in the environment E. The invasion fitness of a rare mutant with strategy y was denoted by Geritz et al. (1998) as

$$s_x(y) = r(y, E_x),$$

where E_x denotes the environment created by the resident phenotype x in the demographic attractor. If $s_x(y) > 0$, the mutant type with the strategy y can invade the resident population (but might not do so because of demographic stochasticity). Conversely, if $s_x(y) < 0$, the mutant type with the strategy y cannot invade the resident population. This process of determining the invasion ability of a mutant is called *invasion analysis*. A related concept is the *fitness gradient*

$$D(x) = \frac{\partial s_x(y)}{\partial y}\Big|_{y=x}.$$

If $D(x) > 0$, mutants with strategy $y > x$ have $s_x(y) > 0$, and the population then evolves towards higher values of strategy x. Conversely, if $D(x) < 0$, the population evolves towards lower values of x. Strategies x^* for which $D(x^*) = 0$ are called *evolutionarily singular strategies*.

In this thesis, we study evolution in discrete-time population models, for which the natural fitness measure is the basic reproduction ratio $R(y, E_x)$, that is, the expected number of offspring produced by an individual. In a population dynamical equilibrium, the two measures are connected so that r and the natural logarithm of R, $\ln R$, are sign equivalent (Mylius and Diekmann, 1995). Specifically, the mutant population will grow if $R(y, E_x) > 1$. Moreover, since even simple discrete-time models of ecological systems can exhibit non-equilibrium between-season dynamics (see, for example, May and Oster (1976)), in this thesis we also study evolution in the case of non-equilibrium population dynamics. In this case the geometric average of the reproduction ratios of different seasons is the correct fitness measure (Lewontin and Cohen (1969), Ferrière and Gatto (1995)). The aim of the studies is to find strategies that are evolutionarily stable.

4.1.3 The ESS concept

As well as the fitness concept, the definition of evolutionary stability has been a topic of much discussion in the previous decades. The concept of an *evolutionarily stable strategy*, or ESS for short, was originally introduced by Maynard Smith and Price (1973) in a game theoretical setting (see also Maynard Smith (1974) and Maynard Smith (1982)). If a whole population has an ESS, no rare mutant with a different trait can increase in numbers. Hence, the name *unbeatable strategy* is also used for the same concept. In terms of the fitness function, a strategy x^* is an ESS if $s_{x^*}(y) < 0$ for all strategies $y \neq x^*$.

However, the definition of the ESS says nothing about whether such a strategy is attracting or not. For this reason, additional terminology has arisen. (Eshel (1996) refers to 18 different terms defining, and sometimes re-defining, various aspects of evolutionary stability.) For example, a strategy x^* is *convergence stable* or an *evolutionary attractor*, if the repeated invasion of nearby mutant strategies to populations with nearby resident strategies will lead to the convergence towards the strategy x^* (Christiansen, 1991). A strategy which is both an ESS and convergence stable is called a *continuously stable strategy*, or CSS (Eshel, 1983). Because evolutionary stability and convergence stability are independent properties, there are four different combinations of them.

4.1.4 The pairwise invasibility plot

The Pairwise Invasibility Plot (Matsuda (1985), van Tienderen and de Jong (1986)), or PIP for short, is a basic graphical tool of the evolutionary analysis of one-dimensional strategies. It shows the sign of the fitness function $s_x(y)$, when the resident strategy x is on the horizontal and the mutant strategy y on the vertical

axis. On the diagonal, $x = y$ and also $s_x(y) = 0$. The PIP shows the points $\{(x, y)|s_x(y) = 0, x \neq y\}$, or zero-isoclines. The evolutionarily singular strategies are located at the points where the zero-isoclines cross the diagonal. For more details on PIPs and their classification, see Geritz et al. (1998).

4.2 Function-valued traits

In this thesis, the assumption of scalar strategies is abandoned. Instead, function-valued strategies (or more precisely measure-valued strategies, since we also allow for Dirac measures) are studied. The adaptive dynamics framework for one-dimensional strategies has nowadays quite a large tool-box (see, for example, Diekmann (2004) for an introduction). However, the analysis becomes significantly more complicated even for vector-valued strategies (see, for example, Heino et al. (1997), Leimar (2001)). For example, pairwise invasibility plots cannot be drawn for higher-dimensional strategies. In particular, the questions concerning convergence stability become very difficult to answer analytically. For this reason, in this thesis we usually only look for evolutionarily stable strategies, and the question of convergence stability is left unanswered.

In nature, many life-history traits are potentially function-valued instead of scalar. Function-valued strategies have been treated in quantitative genetics under the name of *reaction norms* (see, for example, Gomulkiewicz and Kirkpatrick (1992), Gomulkiewicz and Beder (1996), Beder and Gomulkiewicz (1998), Jaffrézic and Pletcher (2000)). However, the models have focused more on genetic detail, and environmental feedback has not been included in them. So far, only a few papers have treated the evolution of function-valued traits in ecological models (see, for example, Dieckmann et al. (2006) for a general review). In this thesis, the evolution of the timing of reproduction is studied. This evolutionary study is primarily related to two separate series of papers. One investigated the optimal clutch size, when reproduction was fixed as a Dirac measure at the end of every reproductive season (Gyllenberg et al., 1996, 1997, to appear). The other series began from a study of male emergence patterns in insects. First, a case of constant environments was treated by Bulmer (1983) and Iwasa et al. (1983), after which the study was generalized to stochastic environments by Iwasa and Haccou (1994), and the ESS conditions were then derived for a more general system by Haccou and Iwasa (1995). However, in this thesis we study an ecological framework different from either of these.

In the current thesis, the evolution of measure-valued strategies is studied by applying the mathematical optimization method called the *calculus of variations*, and the application is based on the following line of reasoning. Assume first that the resident population has an evolutionarily stable strategy. Then, a mutant with a strategy equal to the resident will have zero fitness (i.e., it is neutral with respect to the resident strategy), and any small variation in the mutant strategy around the resident ESS would decrease the fitness. That is, the ESS maximizes the fitness, which is a function of the trait; this is exactly the kind of problem that the calculus

of variations deals with. Parvinen et al. (2006) gives detailed instructions on how to apply the method to evolutionary studies, and, for example, Wan (1995) is a general introduction to the method itself.

5 Main results

The purpose of this thesis is twofold. First, in studies **I**–**III**, mechanistic underpinnings for several discrete-time population models are given. In particular, the studies show how mechanistic population models can be derived in a single, unifying ecological context by systematically varying the details of inter-individual interactions and reproduction. Then, in studies **IV** and **V**, as an example of how evolutionary studies can be carried out in mechanistic models, the evolution of the timing of reproduction is investigated.

5.1 Discrete-time population models with mechanistic underpinnings

Study **I** introduces a population consisting of adults and juveniles of an annual, clonally reproducing species. The dynamics of the population is modelled with a semi-discrete system (as in Section 3.1), so that continuous within-season processes are coupled with discrete between-season dynamics. Within the season, aggressive interactions among adults, among juveniles, and between adults and juveniles are assumed to happen continuously, and they are modelled according to the law of mass action (see Section 3.2). In addition, juveniles are produced either with a constant rate throughout the season or as a Dirac measure situated at a season boundary. When the patterns of inter-individual interaction and reproduction are varied systematically, mechanistic underpinnings can be given for several classical population dynamical models, such as the Beverton and Holt (1957), Hassell (1975), Ricker (1954) and Skellam (1951) models, together with some new discrete-time population models.

As explained in Section 2.4, the Allee effect has great importance in applications to, for example, conservation biology and pest control. However, the modelling framework introduced in study **I** never exhibits the Allee effect. Hence, the purpose of studies **II** and **III** is to derive mechanistic models with the Allee effect. In study **II**, the system introduced in study **I** is modified by assuming sexual reproduction and adding mating processes, thus resulting in several discrete-time population models with the Allee effect. To also include the effects of resource dynamics, in study **III**, the resource-consumer system introduced by Geritz and Kisdi (2004) is modified in a similar manner by adding mating processes. Based on the underlying processes, the models derived in study **II** are more suitable for systems regulated more strongly by inter-individual interactions, whereas the models derived in study **III** might be better at describing systems limited by resource availability.

5.2 Evolution of the timing of reproduction

The evolutionary fate of a specific trait is ultimately determined by the reproductive success of an individual carrying that trait. Because of this, various aspects of reproduction have a central role in the fitness of an individual. (Reviews of life his-

tory evolution can be found in, for example, Roff (1992) and Stearns (1992, 2000). In addition, Harvey et al. (1991) concentrates purely on reproductive strategies.) For this reason, the timing of reproduction is a natural choice for a target trait, and its evolution is investigated in studies **IV** and **V**.

The system introduced in study **I** is used as a modelling framework. Since the purpose of the system was originally to derive discrete-time population models mechanistically, the direct relationship between individual behavior and population dynamics is already available. However, in study **I** the reproductive strategy of individuals was assumed to be fixed, and the study was restricted to either constant reproduction throughout the season or only one, single Dirac measure situated at a season boundary. As a result, study **I** does not answer the question as to which mode of reproduction would be favored by evolution, and this topic is then treated in studies **IV** and **V**. In these studies, then, the trait under investigation is an individual's reproductive strategy. For physiological reasons, the total number of juveniles one adult individual can produce is assumed to be a finite constant, and the aim is to study how this number should be distributed during the season, given the types of inter-individual interactions and mortality processes included in the model. To solve the problem of evolutionary success, we use the ESS concept, and we do this by using invasion analysis.

Since the original system introduced in study **I** also allows non-equilibrium population between-season dynamics, the possibility of fluctuating population densities must be taken into account. Thus, study **IV** treats the simpler case of equilibrium between-season dynamics, and study **V** is a generalization to possibly non-equilibrium situations. In both cases an analog of the Ideal Free Distribution (IFD) arises. (The concept of the IFD was originally introduced by Fretwell and Lucas (1970) and later on elaborated by Fretwell (1972). In short, the standard IFD is a hypothesis concerning the distribution of animal individuals, when they live in an environment consisting of habitats of different quality. The individuals are assumed to be 'ideal' in the sense that they move so as to maximize their fitness, and 'free' in the sense that they are able to enter all the habitats. The IFD hypothesis says that individuals will distribute so that their fitnesses are equalized in different habitats.) In studies **IV** and **V** an IFD arises in the sense that the juveniles' birth moments form an IFD of joint survival probabilities. In both cases, the question as to whether inter-juvenile interactions are included in the model turns out to be crucial. If an ESS exists, it can have an absolutely continuous part only if inter-juvenile interactions are included, whereas in the case of no inter-juvenile interactions only discrete ESSs are possible.

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